

Are stress-free membranes really 'tensionless'?

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In recent years it has been argued that the tension parameter driving the fluctuations of fluid membranes, differs from the imposed lateral stress, the 'frame tension'. In particular, stress-free membranes were predicted to have a residual fluctuation tension. In the present paper, this argument is reconsidered and shown to be inherently inconsistent – in the sense that a linearized theory, the Monge model, is used to predict a nonlinear effect. Furthermore, numerical simulations of one-dimensional stiff membranes are presented which clearly demonstrate, first, that the internal 'intrinsic' stress in membranes indeed differs from the frame tension as conjectured, but second, that the fluctuations are nevertheless driven by the frame tension. With this assumption, the predictions of the Monge model agree excellently with the simulation data for stiffness and tension values spanning several orders of magnitude.

PACS numbers: 87.16.dj, 68.03.Kn, 68.35.Md

Fluid membranes are indispensable constituents of all living things[1]. They are made of self-assembling amphiphilic molecules, mostly lipids, which aggregate to bilayer sheets in an aqueous environment. The fundamental properties of self-assembled membranes have been studied for many decades by experimental studies of simple model membranes, by random interface theories, and by simulations on length scales ranging from the atomic to the mesoscopic scale. Whereas in nature and in typical experimental setups (vesicles, supported membranes), membranes are usually under (slight) tension, most theoretical and simulation studies have focused on the ideal 'tensionless' case.

In the present paper we address a basic question: What is the meaning of 'tensionless' in a membrane? Do theories and simulations/experiments really consider the same object if they refer to tensionless membranes? This has recently been questioned by a number of authors[4–6].

Experimentally and in molecular simulations, the membrane tension is identified with the lateral stress, which is the mechanically accessible quantity. It corresponds to the force which the membrane would exert on a surrounding frame, hence it is also called 'frame tension' σ_f . Membranes are said to be 'tensionless' if $\sigma_f = 0$. In fluctuating membranes, the frame tension is not necessarily identical with the internal membrane tension σ_{int} , i.e., the conjugate variable to the total area in the free energy (at fixed number of lipids), since the local membrane normal fluctuates.

Theoretically, fluctuating membranes are commonly described in terms of effective interface models: The membranes are represented by elastic sheets, subject to an effective potential that depends on their conformation [7]. The simplest and most famous example of such a model is the Helfrich Hamiltonian [8]

$$\mathcal{H}_{\text{Helfrich}} = \int dA \left\{ \sigma_0 + \frac{\kappa}{2} H^2 + \frac{\bar{\kappa}}{2} G \right\} \quad (1)$$

for fluid membranes. Here the integral dA runs over the surface of the sheets, H and G are the total and the Gaussian curvature (i.e., the sum and the product of the inverse principal curvature radii), and κ and $\bar{\kappa}$ are the bending rigidity and the Gaussian rigidity, respectively. The first term with the 'bare tension' σ_0 couples directly to the total surface area A of the membranes. For fluctuating *interfaces* (e.g., between two coexisting fluid phases), this term dominates the effective interface Hamiltonian [9]. In theoretical studies of 'tensionless' *membranes*, σ_0 is often set to zero. The bare tension is related, but again not necessarily identical with the "fluctuation tension" σ_{fluc} , i.e., the coefficient of q^2 in the fluctuation spectrum of a planar membrane[10].

The relation between the externally imposed 'frame tension' σ_f and the internal tension σ_{int} has intrigued scientists for quite some time. In this context, it is important to note that Eq. (1) leaves room for different interpretations. If (1) is taken to describe strictly incompressible membranes with fixed lipid area, but fluctuating number of lipids, σ_0 is proportional to the chemical potential μ_0 for adding a lipid [11]. The number of degrees of freedom N then fluctuates together with the total area A (at fixed A/N). This is the point of view taken by Cai *et al.* in a seminal work of 1994 [11]. At fixed projected area A_p (but fluctuating number of lipids), they argued that the fluctuation tension σ_{fluc} renormalizes to $\sigma_{\text{fluc}} = \sigma_f$ in the thermodynamic limit. More recent authors [2–6] have used a Hamiltonian of the form (1) to describe compressible membranes with fixed number of lipids. In that case, the number of degrees of freedom N is constant and σ_0 is the internal tension[2] σ_{int} . This situation has first been considered by Farago and Pincus in 2003/04, who concluded again $\sigma_{\text{fluc}} = \sigma_f$ for membranes with fixed projected area [2, 3].

This conclusion was recently questioned by Imparato [4] and Fournier and Barbetta [5]. Based on free energy calculations as well as direct calculations of the thermally averaged lateral stress tensor [5] for almost planar inter-

faces (Monge representation, see below), they recover an earlier result by Farago and Pincus regarding the difference between the internal tension σ_{int} and the frame tension σ_f [2], but they argue that the fluctuations are driven by σ_{int} . The fluctuation tension is predicted to be always larger than the frame tension. Most notably, stress-free membranes with $\sigma_f = 0$ are predicted to have a residual fluctuation tension $\sigma_{\text{fluc}}^{(0)} = k_B T N / A$, where N is the number of fluctuation degrees of freedom. The residual tension can be attributed to the contribution of the fluctuations on the interfacial free energy. On large length scales, it should dominate the fluctuation spectrum.

Experimentally, however, the evidence for such an effect is scarce. In experiments, the effect of fluctuations can be measured by monitoring the relative excess area $\langle (A - A_p) / A_p \rangle$, and the frame tension σ_f can be imposed, e.g., by the Laplace pressure in micropipette experiments [12, 13]. The experimental findings in such setups were consistent with the assumption $\sigma_{\text{fluc}} = \sigma_f$. A difference between σ_{fluc} and σ_f was only reported in one recent study of giant vesicles [14], where σ_{fluc} was inferred from the amplitude of fluctuations and σ_f from the shape of the vesicles on surfaces.

Likewise, most simulations of fluctuating stress-free membranes [15–21] or membrane stacks [22] could be described very satisfactorily by elastic theories for $\sigma_{\text{fluc}} = 0$, *i.e.*, the long-wavelength behavior is apparently dominated by bending modes. This holds for simulations of atomistic [16, 17] as well as coarse-grained [15, 18–22] models, with two exceptions: In simulations of membranes under varying stress, Imparato [4] and Stecki [23] independently report the fluctuation tension σ_{fluc} to be larger than the frame tension σ_f over a range of frame tensions, in agreement with the theoretical prediction. In contrast, a more recent coarse-grained simulation study by Neder *et al.* [24] yielded $\sigma_{\text{fluc}} = \sigma_f$ within the error at moderate frame tensions and $\sigma_{\text{fluc}} < \sigma_f$ at extreme tensions. A *reduction* of σ_{fluc} compared to σ_f cannot be explained by any available theory. On the other hand, the membrane was also found to exhibit substantial structural changes in this high tension regime, which presumably accounts for part of the effect.

In sum, the majority of experimental and numerical evidence so far points towards $\sigma_{\text{fluc}} = \sigma_f$ at low tensions, and against the existence of a residual fluctuation tension in stress-free membranes. On the other hand, neither the simulation data nor the experimental data were accurate enough to unambiguously exclude that possibility. It should be noted that the elastic parameters extracted from molecular simulation data can be severely affected by the short-wavelength fluctuations, especially in small systems. In order to avoid this problem, Fournier and Barbetta have carried out simulations of a discretized fluctuating line ‘membrane’ in two spatial dimensions. Their results not only clearly showed an effect [5], but also indicated that the fluctuation tension σ_{fluc} differs

substantially from *both* the internal and the frame tension, σ_{int} and σ_f . The total length of the line (*i.e.*, the interfacial ‘area’) in this study was allowed to fluctuate freely, only controlled by the internal tension σ_{int} .

Historically, the overwhelming theoretical literature on ‘tensionless’ fluctuating fluid membranes relies on the assumption that the fluctuation tension is zero. On the other hand, the physically (*i.e.*, mechanically) relevant tension is obviously the frame tension. If the frame tension and the fluctuation tension are not identical, a vast body of work has to be revisited. Therefore, a clarification of the issue is clearly desirable. The purpose of the present work is to contribute to such a clarification. We will first re-analyze the theory and conclude that the central result, $\sigma_{\text{fluc}} \neq \sigma_f$, is less rigorous than it seems. Then we will present numerical results which strongly support the hypothesis that the frame tension and the fluctuation tension are in fact equal for membranes with fixed number of lipids and fixed area.

The starting point of the previous studies [4, 5] is the Monge representation for planar membranes [7] with fluctuating area and fixed number of lipids. The membrane is assumed to fluctuate only weakly about a plane, such that the local membrane position can be parameterized by a function $h(x, y)$ with the constraint $\iint dx dy h(x, y) = 0$. Furthermore, the Hamiltonian is expanded in powers of h and only quadratic terms are taken into account. Omitting the contribution of the Gaussian curvature, which is constant for closed membranes with fixed topology, one obtains [7]

$$\mathcal{H}_{\text{Monge}} = \sigma_0 A_p + \frac{1}{2} \int_{A_p} dx dy \{ \sigma_0 (\nabla h)^2 + \kappa (\Delta h)^2 \}, \quad (2)$$

where the integral runs over the projected area A_p of the membrane. Since the ensemble under consideration is one with fixed number of lipids, σ_0 is the internal tension σ_{int} . Furthermore, the height fluctuations in this linearized model are clearly driven by σ_0 , *i.e.*, $\sigma_{\text{fluc}} = \sigma_0 = \sigma_{\text{int}}$.

To fully define the Monge model, one needs to specify two additional parameters: The in-plane and perpendicular coarse-graining lengths Λ and λ , respectively, usually taken to be of the order of the membrane thickness. The parameter Λ acts as a small-wavelength cutoff and determines the number of fluctuation degrees of freedom N via $N = A_p / \Lambda^2$. Following Refs. 2–5, we will assume that N is proportional to the number of lipids.

For future reference, we explicitly point out the approximation $\sqrt{1 + (\nabla h)^2} \approx (1 + (\nabla h)^2 / 2)$ entering the expression (2). The Monge model thus approximates the full Hamiltonian for planar interfaces up to the order $(\nabla h)^2 \sim (A - A_p) / A_p$.

Throughout the remaining paper, energies will be given in units of $k_B T$. The partition function of the Monge model can be evaluated analytically, giving the free energy

$$G(N, \sigma_{\text{int}}, A_p) = \sigma_{\text{int}} A_p + \frac{(N-1)}{2} \left(\ln(2\sigma_{\text{int}} \lambda^2) - 2 \right) \quad (3)$$

$$+ \left(1 + \frac{\sigma_{\text{int}} A_p}{4\pi\kappa(N-1)} \right) \ln \left(1 + \frac{4\pi\kappa(N-1)}{\sigma_{\text{int}} A_p} \right)$$

The only approximation entering this result was to replace the sum $\sum_{\vec{k}} f(|\vec{k}|)$ in Fourier space \vec{k} by the integral $\frac{A_p}{2\pi} \int_0^{k_{\text{max}}} dk f(k)$, where the value $k_{\text{max}} = \sqrt{4\pi \frac{N-1}{A_p}}$ is imposed by the requirement $\sum_{\vec{k} \neq 0} = N-1$.

Eq. (3) gives the interfacial free energy of a fluctuating interface with fixed projected area A_p and fluctuating total area A , controlled by the internal tension σ_{int} . Membranes are better described by an ensemble where A_p fluctuates, controlled by the frame tension σ_f , and A is fixed. In Refs. [2–5], it is argued that these different ensembles are equivalent and the appropriate free energy $\tilde{G}(N, A, \sigma_f)$ can be obtained by a Legendre transform. Here the number of degrees of freedom N is still fixed, because the number of lipids in the membrane is fixed. Without having to determine \tilde{G} explicitly, one can easily calculate the relation between the frame tension and the internal tension *via* $\sigma_f = \frac{\partial G}{\partial A_p}$, giving

$$\sigma_f = \sigma_{\text{int}} \left(1 + \frac{1}{8\pi\kappa} \ln \left(1 + \frac{4\pi\kappa(N-1)}{\sigma_{\text{int}} A_p} \right) \right) - \frac{(N-1)}{2A_p}. \quad (4)$$

This reproduces the result in Refs. [2, 4, 5] and demonstrates the existence of a residual internal tension, $\sigma_{\text{int}} \sim N-1/2A_p$, at $\sigma_f = 0$. Likewise, the total area is related to σ_{int} and A_p by

$$A = \frac{\partial G}{\partial \sigma_{\text{int}}} = A_p \left(1 + \frac{1}{8\pi\kappa} \ln \left(1 + \frac{4\pi\kappa(N-1)}{\sigma_{\text{int}} A_p} \right) \right) \quad (5)$$

Inverting this relation and expressing σ_{int} as a function of A and A_p , one can rewrite the ratio $\sigma_f/\sigma_{\text{int}}$ entirely as a function of $(A - A_p)/A_p$, giving

$$\frac{\sigma_f}{\sigma_{\text{int}}} = 1 - \frac{1}{8\pi\kappa} (e^y - 1 - y) \approx 1 - 4\pi\kappa \left(\frac{A - A_p}{A_p} \right)^2 + \dots \quad (6)$$

with $y = 8\pi\kappa(A - A_p)/A_p$. In the last step, we have expanded $\sigma_f/\sigma_{\text{int}}$ in powers of the excess area $(A - A_p)/A_p$.

Hence the frame tension is found to differ from the internal tension to second order in $(A - A_p)/A_p$. On the other hand, the Monge model approximates planar interfaces only up to the first order in $(\nabla h)^2$ or $(A - A_p)/A_p$. Thus the results (6) and (4) are not rigorous! Whatever the differences between σ_f , σ_{fluc} , and σ_{int} in real membranes are, it is not possible to determine them within the Monge model.

Another serious issue is the equivalence of ensembles, which was taken for granted in the above derivation. Different ensembles are only equivalent in the thermodynamic limit of infinite membranes $A \rightarrow \infty$ at fixed A/N . At zero tension, this limit does not exist within the

Monge model, since tensionless membranes bend around on length scales larger than the persistence length and are no longer planar. Hence the thermodynamic limit is generally questionable for membranes in the floppy low-tension regime.

One can also derive directly a Monge approximation for planar membranes in the desired (N, A, σ_f) ensemble. The Hamiltonian would then read $\mathcal{H} = -\sigma_f A_p + \mathcal{H}_{\text{bending}}$, where the second term $\mathcal{H}_{\text{bending}}$ includes the pure bending contributions, and fluctuations are subject to the constraint that A is constant. Expanding again in powers of h up to quadratic order, one obtains [25]

$$\mathcal{H}'_{\text{Monge}} = -\sigma_f A + \frac{1}{2} \int_{A_p} dx dy \{ \sigma_f (\nabla h)^2 + \kappa (\Delta h)^2 \}. \quad (7)$$

According to this alternative Ansatz, the fluctuations are driven by the *frame* tension. This result is also only valid up to order $(A - A_p)/A_p$, like Eq. (6). The Monge model can hence be used both to predict equivalence and non-equivalence of σ_{fluc} and σ_f !

The question remains which is correct. To shed light on this issue, the present author has carried out numerical Monte Carlo simulations of one-dimensional 'membranes' in two-dimensional space. The model is similar to that of Fournier and Barbetta [5], except that the membranes had fixed interfacial 'area', *i.e.*, fixed contour length L . Compared to two-dimensional surfaces, one-dimensional membranes have the advantage that the Helfrich Hamiltonian, Eq.(1), can be discretized in a straightforward manner, without having to resort to sophisticated models methods like randomly triangulated sheets [26]. Moreover, fluctuation effects are stronger in two dimensions than in three dimensions, hence they can be studied more easily.

To set the stage, we briefly repeat the previous calculations up to Eq. (6) for membranes in two-dimensional space. 'Membranes' are then simply lines with total length L and projected length L_p . Otherwise, the Monge model is constructed in the same way as in Eq. (2), with a height function $h(x)$. The equivalent of Eq. (3) reads

$$G(N, \sigma_{\text{int}}, L_p) = \sigma_{\text{int}} L_p + \frac{N-1}{2} \ln \left(\frac{\lambda^2 \sigma_{\text{int}}^2 L_p}{2\pi\kappa(N-1)} \right) \quad (8)$$

$$+ \sum_{k=1}^{N/2} \ln \left(\frac{(\pi k)^2}{\tilde{\sigma}} \left(1 + \frac{(\pi k)^2}{\tilde{\sigma}} \right) \right),$$

where we have introduced the dimensionless rescaled tension $\tilde{\sigma} = \sigma_{\text{int}} L_p^2 / 4\kappa$. We note that in two dimensions, the sum \sum_k may not be replaced by an integral, because it is dominated by the contributions at small k .

The total 'area' L and the frame tension σ_f can again be determined by taking the appropriate derivatives of the free energy, $L = \partial G / \partial \sigma_{\text{int}}$ and $\sigma_f = \partial G / \partial L_p$. After some algebra, and approximating $\sum_{k=1}^{N/2} (1 + (\frac{\pi k}{x})^2)^{-1} \approx$

$\sum_{k=1}^{\infty} (1 + (\frac{\pi k}{x})^2)^{-1} = \frac{1}{2}(x \coth(x) - 1)$, one obtains

$$L - L_p = \frac{L_p^2}{24\kappa} \frac{3}{\tilde{\sigma}} (\sqrt{\tilde{\sigma}} \coth(\sqrt{\tilde{\sigma}}) - 1) \quad (9)$$

$$\sigma_f - \sigma_{\text{int}} = \frac{1}{L_p} (\sqrt{\tilde{\sigma}} \coth \sqrt{\tilde{\sigma}} - 1) - \frac{3(N-1)}{2L_p}. \quad (10)$$

which takes the value $\sigma_f - \sigma_{\text{int}} = -3(N-1)/2L_p$ at $\tilde{\sigma} \rightarrow 0$. In two dimensions, $\sigma_f/\sigma_{\text{int}}$ as a function of $(L - L_p)/L_p$ has an essential singularity at $(L - L_p)/L_p \rightarrow 0$. Therefore, we cannot give a rigorous expansion as in Eq. (6), but we can only derive an approximate expression for the regime $\coth(\sqrt{\tilde{\sigma}}) \approx 1$,

$$\frac{\sigma_f}{\sigma_{\text{int}}} \approx 1 + 2 \frac{L - L_p}{L_p} - 24\kappa \frac{N-1}{L_p} \left(\frac{L - L_p}{L_p} \right)^2 + \dots, \quad (11)$$

which shows that $\sigma_f/\sigma_{\text{int}}$ significantly deviates from one in two dimensions (*i.e.*, the deviation is linear in the small parameter $(L - L_p)/L_p$).

For future reference, we also give the expression for the squared amplitude of fluctuations $w^2 = \langle h^2 \rangle - \langle h \rangle^2$, which was obtained by direct evaluation of the statistical average:

$$w^2 = \frac{L_p^3}{720\kappa} \frac{45}{\tilde{\sigma}^2} \left(\frac{\tilde{\sigma}}{3} + 1 - \sqrt{\tilde{\sigma}} \coth(\sqrt{\tilde{\sigma}}) \right). \quad (12)$$

This completes the summary of results for the Monge model in two dimensions. Given the previous discussion, we would not expect them to be of much use, because they are only valid to linear order in $(L - L_p)/L_p$ and they have been calculated for the wrong ensemble $((N, \sigma_{\text{int}}, L_p)$ as opposed to (N, L, σ_f)). The ensembles can only be expected to be equivalent in the thermodynamic limit $L_p \rightarrow \infty$ at fixed N/L_p , corresponding to $\tilde{\sigma} \rightarrow \infty$, which is a very special limit in the above equations. Surprisingly, it will turn out that the equations nevertheless describe the simulation data remarkably well.

In the numerical simulations, membranes with fixed total length L were split in N segments of fixed length L/N , and a frame tension σ_f was imposed in the x -direction. The discretized Hamiltonian reads

$$\mathcal{H} = -\sigma_f L_p + \kappa \frac{N}{L} \sum_{i=1}^N (1 - \vec{e}_i \cdot \vec{e}_{i-1}), \quad (13)$$

where the sum i runs over the segments, \vec{e}_i denotes the unit vector in the direction of the i th segment, L_p is the projected length ($L_p = \frac{L}{N} \sum_i e_{i,x}$), and periodic boundary conditions were applied in the x direction. Monte Carlo simulations were carried out for two discretizations, $N = 40$ and $N = 100$, and parameters κ/L and $\sigma_f L$ ranging from $\kappa/L = 1$ to $\kappa/L = 1000$ and $\sigma_f L = 0$ and $\sigma_f L = 0.05$ to $\sigma_f L = 10000$. Typical run lengths were $0.5 - 1.0 \cdot 10^9$ Monte Carlo steps. Since the results are compared with the predictions of the Monge

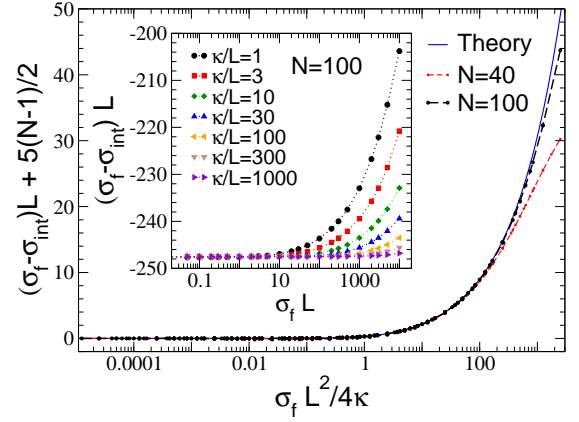


FIG. 1: Difference between internal tension σ_{int} and frame tension σ_f vs. frame tension σ_f . Inset: Raw data for discretization $N = 100$ and selected values of the stiffness κ . Main frame: Rescaled data for two discretizations N and all values of κ ($\kappa/L = 1, 2, 3, 5, 10, 15, 20, 30, 50, 100, 200, 300, 500, 1000$), vs. rescaled tension $\hat{\sigma} = \sigma_f L^2 / 4\kappa$, compared with the theoretical master curve $f(x) = \sqrt{x} \coth(\sqrt{x}) - 1$ from Eq. (10)

model, parameter combinations (κ, σ_f) were disregarded for which more than $1/1000$ of segments had angles larger than 45° with the x -axis. This applied to $\kappa/L \leq 1$ at frame tensions $\sigma_f L \leq 30$. From the simulation data, one can extract in a straightforward manner the statistically averaged projected length, $\langle L_p \rangle$, the squared amplitude of fluctuations, $\langle w^2 \rangle$, and the internal tension $\sigma_{\text{int}} = -\partial \tilde{G} / \partial L = -\langle \partial \mathcal{H} / \partial L \rangle + 2(N-1)/L$, where $\tilde{G}(N, L, \sigma_f)$ is the free energy of the system [27]

Fig. 1 summarizes the results for the internal tension. The bare data in the inset clearly show that the internal tension deviates from the applied frame tension, as predicted by Eq. (10). The value of the residual tension at $\sigma_f \rightarrow 0$ however disagrees with the theory. Whereas Eq. (10) predicts $\sigma_{\text{int}} L |_{\sigma_f=0} \approx 3(N-1)/2$, the actual data rather suggest $\sigma_{\text{int}} L |_{\sigma_f=0} = 5(N-1)/2$. The additional term $(N-1)/2$ can be attributed to the translational freedom of the segments along the x -direction.

Next we test whether the data for $(\sigma_f - \sigma_{\text{int}})L_p + 3(N-1)/2$ can be scaled in a way that they collapse onto a single curve for all values of κ , σ_f , and N . Eq. (10) suggests to try the scaling variable $\tilde{\sigma} = \sigma_{\text{int}} L_p^2 / 4\kappa$. It turns out that the data do not scale at all with this Ansatz. The scaling is much better with the scaling variable $\sigma_f L_p^2 / 4\kappa$, but still not perfect (data not shown). If one however replaces L_p by L everywhere and uses the scaling variable $\hat{\sigma} = \sigma_f L^2 / 4\kappa$, the data collapse almost perfectly onto the theoretical master curve suggested by Eq. (10) for all values of κ and σ_f and both discretizations N . Only for large values of $\hat{\sigma}$ does one observe deviations, which can be attributed to discretization effects since they become smaller for larger N (Fig. 1, main frame).

These first findings already suggest that the relevant quantity driving the fluctuations is the frame tension,

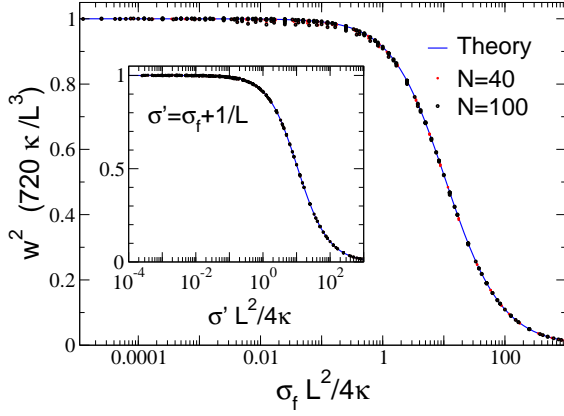


FIG. 2: Scaling plots of the squared amplitude of fluctuations w^2 vs. rescaled tension $\hat{\sigma} = \sigma_f(L^2/4\kappa)$ compared with the theoretical master curve $f(x) = \frac{45}{x^2}(\frac{x}{3} + 1 - \sqrt{x} \coth(\sqrt{x}))$ (Eq. (12)). Inset shows an alternative scaling plot where σ_f in $\hat{\sigma}$ is replaced by $\sigma' = \sigma_f + 1/L$.

not the internal tension. Furthermore, they also suggest that the relevant *length* scale in the system is the total length L , not the projected length L_p . With the corresponding replacements, the results are in surprisingly good agreement with the predictions of the Monge model, despite the fact that the latter have been derived for a different ensemble with different scaling variables. We will now proceed to investigate two quantities that probe the fluctuations directly, *i.e.*, the squared amplitude of fluctuations w^2 and the excess length $(L - L_p)$. These quantities characterize the fluctuations in an integrated way.

Fig. 2 shows scaling plots for the squared amplitude of fluctuations. The data are rescaled as suggested by Eq. (12), with L_p replaced by L and plotted against the rescaled frame tension $\hat{\sigma}$. The scaling is quite good, but not perfect. It can be improved by shifting σ_f by the small amount $\delta\sigma = 1/L$ (see inset of Fig. 2). The data then collapse very nicely onto the theoretical curve predicted by (12). No data collapse is obtained when plotting against the rescaled *internal* tension σ_{int} (not shown). Thus the results for the squared amplitude of fluctuations indicate that the fluctuations are driven by the frame tension σ_f , possibly slightly shifted, and not by the internal tension σ_{int} . The results for the excess length $(L - L_p)$ support this conclusion (Fig. (3)). In that case, the best scaling is achieved directly with $\hat{\sigma} = \sigma_f(L^2/4\kappa)$, without additional shift. The data again collapse excellently onto the theoretical master curve suggested by Eq. (9).

In sum, the simulation data show clearly that the membrane fluctuations are driven by the frame tension σ_f . These results raise the question why Barbetta and Fournier in Ref. [5] obtained a different result from simulations of essentially the same model. The answer is that these simulations were carried out in a different ensemble where both the contour length and the projected

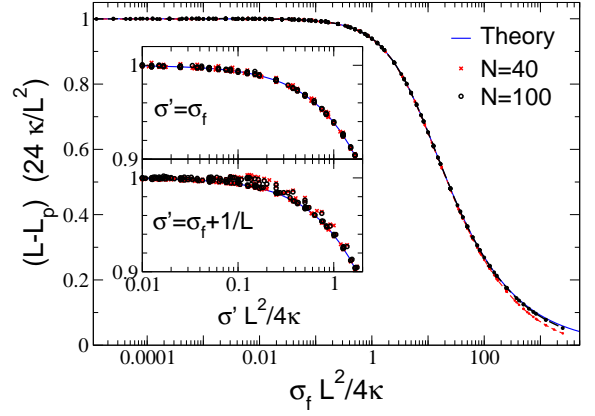


FIG. 3: Scaling plot of the excess length $\langle(L - L_p)\rangle$, vs. rescaled tension $\hat{\sigma} = \sigma_f(L^2/4\kappa)$, compared with the theoretical master curve, $f(x) = \frac{3}{x}(\sqrt{x} \coth(\sqrt{x}) - 1)$ (Eq. (9)). Inset compares the scaling with shifted and unshifted σ' in the most critical parameter region.

length were allowed to fluctuate, *i.e.*, the $(N, \sigma_{\text{int}}, \sigma_f)$ ensemble as opposed to the (N, L, σ_f) ensemble considered in the present work. As pointed out earlier, the ensembles are not equivalent. To further analyze the issue, additional simulations were carried out for membranes in the (N, L, L_p) ensemble and in the $(N, \sigma_{\text{int}}, L_p)$ ensemble. The purpose of these simulations was to find out whether the fluctuations in other ensembles might be driven by σ_{int} instead of σ_f .

Fig. 4 shows the squared amplitude of fluctuations w^2 vs. the excess length $(L - L_p)$, in a scaling plot which is independent of the actual choice of the rescaled tension. The data are taken from simulations in the (N, L, σ_f) ensemble and in the (N, L, L_p) ensemble. In the (N, L, σ_f) ensemble, they collapse onto a single curve which agrees nicely with the theoretical prediction from Eqs. (9) combined with (12). The data from the (N, L, L_p) ensemble also collapse, but the scaling curve is different and not consistent with Eqs. (9) and (12) [28].

If L is allowed to fluctuate, the situation is further complicated by the fact that in one dimension, the total bending energy of bubbles decreases with increasing bubble size. As a consequence, the simulation data in the $(N, \sigma_{\text{int}}, L_p)$ ensemble feature a transition between a flat state and an inflated bubble state at bending stiffness $\kappa/L \sim 3$ and low tensions (data not shown). The simulations of Fournier and Barbetta were carried out at $\kappa/L = 2.5$ (in yet another ensemble), hence the vicinity of a similar transition possibly accounts for some of the intriguing phenomena reported in Ref. 5.

In the introduction, we have raised the question whether theories and simulations/experiments really consider the same object if they refer to 'tensionless' membranes? Based on the simulation results presented above, we conclude that the answer is most likely "yes". At least in one dimensional membranes with fixed 'area', the fluc-

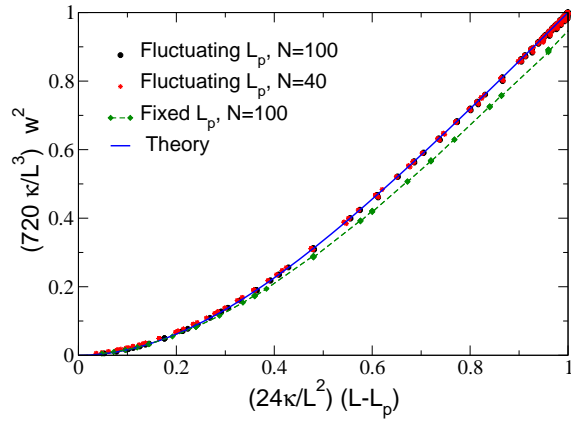


FIG. 4: Rescaled squared amplitude of fluctuations vs. excess length. Circles and stars correspond to data for fluctuating projected length L_p and discretizations $N = 40$ and $N = 100$, respectively. Diamonds correspond to data from simulations with fixed projected length L_p . The solid line shows the theoretical prediction from Eq. (9) combined with Eq. (12). The dashed line is a guide for the eye.

tuations are driven by the imposed lateral stress, and the behavior of stress-free (tensionless) membranes is consistent with that of the Monge model at tension zero. These results will presumably also hold for two-dimensional membranes. We have presented an argument in Eq. (7) that rationalizes the prediction $\sigma_{\text{fluc}} = \sigma_f$ in the physically relevant (N, A, σ_f) ensemble for arbitrary dimensions. We should note, however, that our numerical simulations indicate that the relevant length scale is the total 'area' rather than the projected 'area'. This presumably renormalizes the actual ' q^2 coefficient', $\sigma_{\text{fluc}} = \sigma_f (L_p/L)^2$ in two dimensions [29], or $\sigma_{\text{fluc}} = \sigma_f (A_p/A)$ in d dimensions. A detailed analysis of the full fluctuation spectra as a function of the wavevector q will be presented elsewhere.

The present author hopes that this paper will stimulate discussions and further work on these intriguing and important issues. For example, it is not clear why the Monge model provides such a good prediction of the scaling *functions* for the various quantities, even though it is derived for the wrong ensemble with different scaling *variables*. Furthermore, mesoscopic simulations of two-dimensional fluctuating fluid sheets, *e.g.*, using randomly triangulated surfaces [26] or Fourier techniques [30], would clearly be desirable.

The author thanks J. Neder, J.-B. Fournier and M. Weigl for inspiring discussions. Partial support from the German Science Foundation (CRC 625) is gratefully acknowledged.

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